

Elongated chambers for field studies across atmospheric CO₂ gradients

H. B. JOHNSON, H. W. POLLEY and R. P. WHITIS

Grassland, Soil and Water Research Laboratory, U.S. Department of Agriculture, Agricultural Research Service, 808 E. Blackland Road, Temple, TX 76502, USA

Summary

1. We describe a field facility that controls CO₂ along continuous gradients from superambient to subambient concentrations. The facility consists of two transparent, tunnel-shaped chambers, each 1-m wide and tall and 60-m long. Pure CO₂ is injected into one chamber during daylight to initiate a superambient CO₂ gradient (550–350 $\mu\text{mol mol}^{-1}$). Ambient air is introduced to the second chamber to initiate a subambient CO₂ gradient (350–200 $\mu\text{mol mol}^{-1}$). CO₂ concentrations at night are regulated at 150 $\mu\text{mol mol}^{-1}$ above daytime values along each gradient. The CO₂ gradients are maintained by varying the rate and direction (day/night) of air flow.
2. Air temperature and vapour pressure deficit are regulated near ambient values by cooling and dehumidifying air at 5-m intervals along chambers.
3. Desired CO₂ gradients were regulated on grassland for virtually the entire 9-month growing season in 1998, including a 6-month drought. Consistent CO₂ concentrations were maintained along gradients despite seasonal variation in species composition, leaf area, and temperature.
4. Daytime temperatures in chambers tracked the seasonal pattern in 1998. The polyethylene covering on chambers transmitted 90% of incident light, but usually increased the ratio of diffuse to direct light.
5. By enabling the study of trends in plant and ecosystem responses to CO₂ over both subambient and superambient concentrations, elongated chambers fill a void in CO₂ research facilities.

Key-words: Air temperature, photosynthesis, respiration, vapour pressure deficit

Functional Ecology (2000) **14**, 388–396

Introduction

Atmospheric CO₂ concentration is projected to double during the next century (Alcamo *et al.* 1996). The urgent need to predict the consequences of this change has led to steady innovation in facilities used to study CO₂ effects. Facilities that provide CO₂ enrichment to field plots for extended periods and that have minimal influence on light, temperature and other environmental variables have been developed (e.g. Allen *et al.* 1992; Leadley *et al.* 1997; Norby *et al.* 1997; Hendrey *et al.* 1999). With increasing sophistication, however, has come increasing expense (Kimball 1992). Partly as a result, enrichment studies rarely consider more than two CO₂ concentrations. Non-linear or threshold responses of plants and ecosystems that may be critical to future dynamics go undetected (Ackerly & Bazzaz 1995; Körner 1995).

Results from a limited number of mostly greenhouse and growth-chamber experiments indicate that plants

are more responsive to CO₂ changes at the subambient concentrations of the past than at the elevated concentrations forecast for the future (Baker, Allen & Boote 1990; Allen *et al.* 1991; Polley, Johnson & Mayeux 1992; Dippert *et al.* 1995; Polley *et al.* 1996). Consequently, past increases in CO₂ have been implicated in such regional and global phenomena as increases in forest production and tree turnover rates (Phillips & Gentry 1994), increases in agricultural production (Mayeux *et al.* 1997), and vegetation change (Mayeux, Johnson & Polley 1991; Johnson, Polley & Mayeux 1993; Ehleringer, Cerling & Helliker 1997; Street-Perrott *et al.* 1997). Though plausible given current evidence, few of these predictions have been tested under realistic field conditions.

Rising CO₂ is but one of a myriad of changes affecting ecosystems. The most reliable experiment for predicting CO₂ effects on the biosphere may be the real-world experiment of the last two centuries. The lack of field data over subambient concentrations

limits our ability to place the influence of CO₂ in context with other changes (e.g. changes in fire regimes, grazing management and human population density).

Here we describe and document the performance of chambers constructed on grassland that provide reproducible control of CO₂ along continuous gradients from superambient to subambient concentrations. This field facility is designed for small-statured vegetation (< 1 m height) and is modelled after a prototype chamber that has been operated in a glasshouse to maintain subambient CO₂ concentrations (Mayeux *et al.* 1993). These field chambers incorporate the basic design and many of the control systems of the prototype, but include two significant improvements.

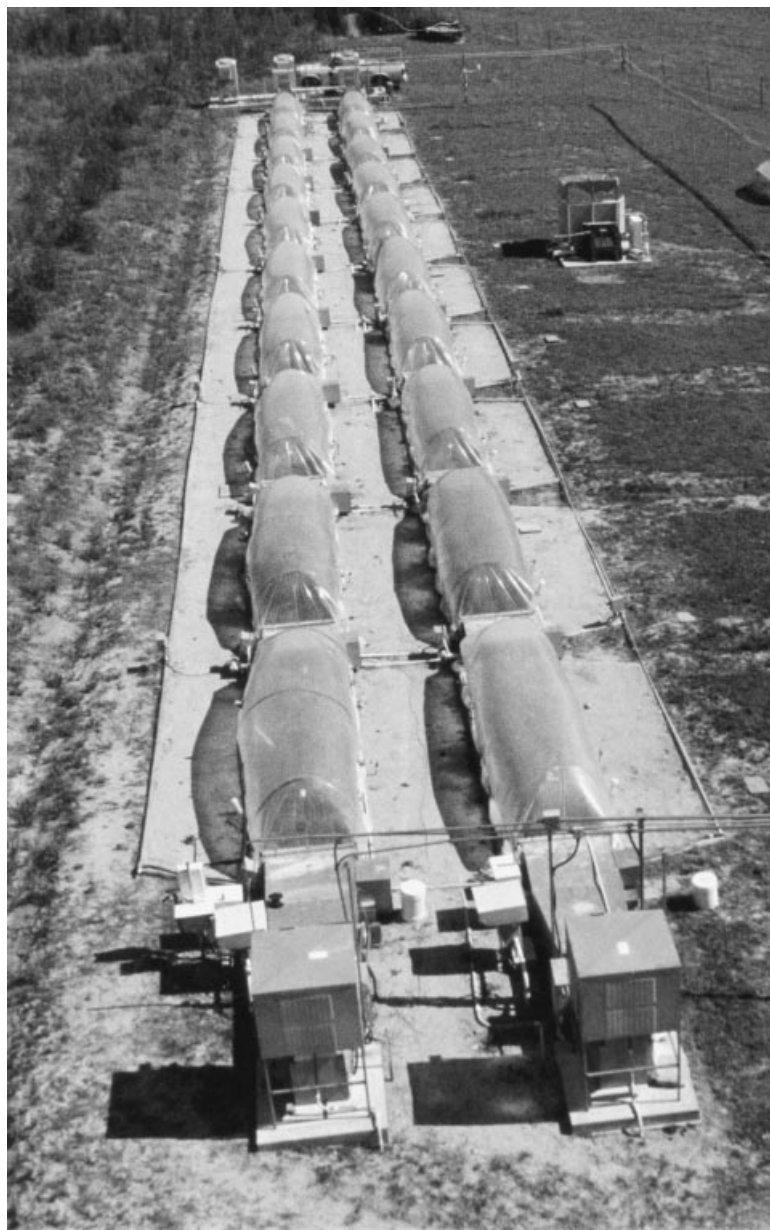


Fig. 1. Aerial view from the south of a field facility used to expose grassland to a continuous gradient in CO₂ concentration. In the foreground are two blower housings. Heat exchangers used to cool and dehumidify chamber air are located to the north of the chambers (top of photograph).

Hardware and control and monitoring systems were added (1) to elevate the CO₂ concentration of air input to chambers and (2) to regulate CO₂ concentration at night. With these improvements, long-term studies can be conducted under realistic field conditions to address two of the major needs of CO₂ research: (1) evidence for the shape of the response curve of plants and ecosystems to CO₂ concentration, and (2) evidence for effects of past changes in CO₂ on 'natural' ecosystems.

Materials and methods

The elongated chambers described here depend entirely upon photosynthesis during daylight and upon respiration at night to create CO₂ gradients. Air introduced into chambers during daylight is progressively depleted of CO₂ by photosynthesizing plants as it is moved by a blower towards the air outlet of the system. The direction of air flow is reversed at night, and respiration by the enclosed ecosystem progressively increases the CO₂ concentration of chamber air. Desired CO₂ concentration gradients are maintained by automatically varying the rate of air flow through chambers in response to changes to the rates of photosynthesis (daylight) or respiration (night). This results in daytime and night-time CO₂ gradients that are nearly parallel, an improvement in design over the prototype chamber in which CO₂ was not regulated at night (Mayeux *et al.* 1993).

CHAMBER DESCRIPTION

The controlled-environment facility was constructed on a grassland in central Texas (31°05' N, 97°20' W) dominated by the C₄ perennial grass *Bothriochloa ischaemum* (L.) Keng and C₃ perennial forbs *Solanum dimidiatum* Raf. and *Ratibida columnaris* (Sims) D. Don. It consists of two tunnel-shaped chambers aligned parallel along a north to south axis (Fig. 1; see Table 1 for list of equipment and vendors). Each chamber is 1 m wide and tall and 60 m long. Chambers are divided into a series of 10 5-m long compartments, each of which is separated from adjacent compartments by 1 m × 1 m sheet-metal ducts containing chilled-water cooling coils (Fig. 2). Aerial growth of vegetation in each 5-m compartment is enclosed in a transparent polyethylene film attached to wooden timbers embedded in the soil surface. The polyethylene film is supported by rounded bows, and is attached at the ends of the 5-m compartments to the 0.25-m tall ducts. Soil is isolated to a depth of 0.9 m from surrounding soil with a rubber-coated fabric attached to timbers. Water equivalent to the amount of rainfall is added through a metered surface irrigation system on the day following a precipitation event. The soil surface in the 1.5-m wide space between chambers and in the area extending to about 1 m beyond the outside of each chamber is covered with

Table 1. Vendors of equipment used in elongated chambers

| Equipment | Make/model | Vendor |
|-----------------------------------------------------|----------------------------------------------------|-----------------------------------|
| Polyethylene film | Dura-Film/Super Dura 4 | AT Plastics, Toronto, Canada |
| Blower motor/controller | 2M168C/4Z829 | Dayton Electric, Lake Forest, IL |
| Silicon photodiode | LI-190SB | Li-Cor, Lincoln, NE |
| Infrared CO ₂ /H ₂ O analyser | LI-6262 | Li-Cor, Lincoln, NE |
| Vacuum pumps | VP 0660 | Grace Air Components, Houston, TX |
| Dew-point generator | LI-610 | Li-Cor, Lincoln, NE |
| Pressure indicator | DPI 260 | Druck Inc., New Fairfield, CT |
| Weather station | CR-21X and related equipment | Campbell Scientific, Logan, UT |
| Heat exchanger | HX-2000 | Neslab, Portsmouth, NH |
| Microloggers, multiplexers | CR-7, CR-10, CR-21X, SDM-AO4, SDM-CD16AC, AM25T | Campbell Scientific, Logan, UT |

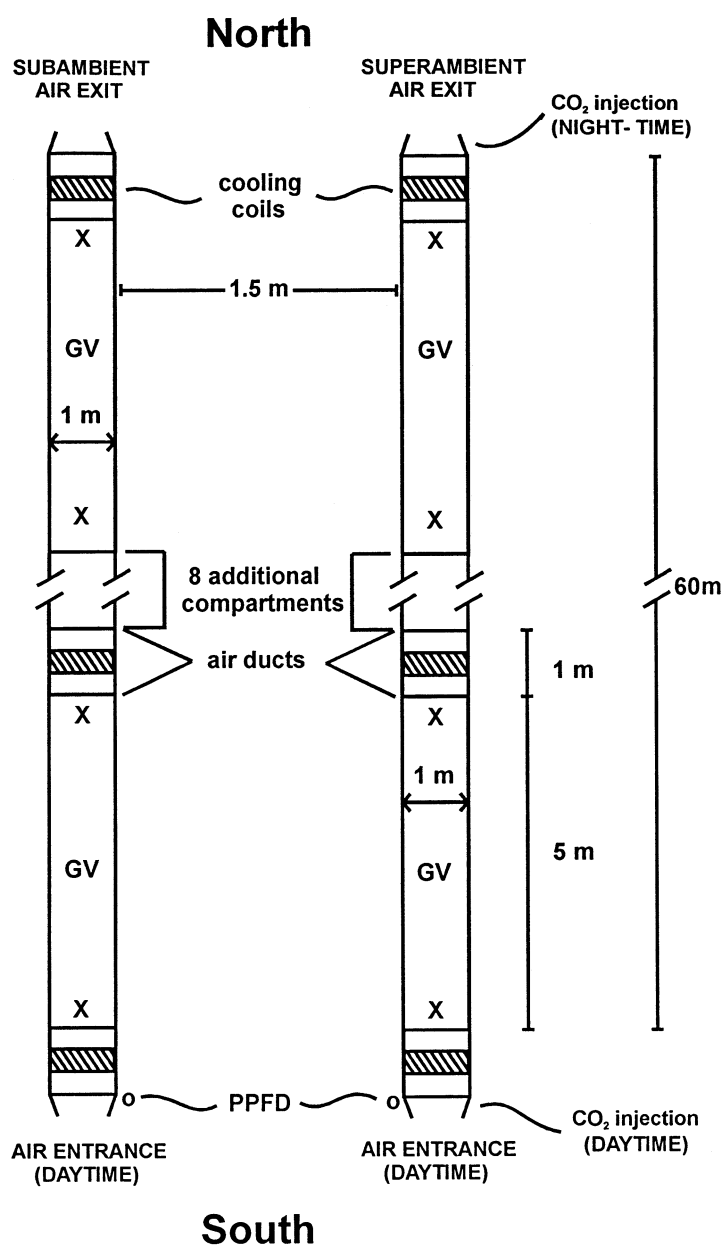


Fig. 2. Schematic of elongated chambers indicating points of CO₂ injection and sampling locations for PPFD (o) and for CO₂, dew-point, and temperature (X). Illustrated are the initial and final 5-m compartments of each 60-m long chamber that enclose grassland vegetation (GV).

a shallow layer of sand to facilitate all-weather foot traffic (Fig. 1).

MONITORING AND CONTROL OF CO₂

Air is forced through ducts containing cooling coils and into each 60-m long chamber by belt-driven cylindrical blowers with an air flow capacity of 1300 l s^{-1} in free air. Air is introduced during daylight with blowers mounted at the south end of each chamber. Blowers at the north end of each chamber are used to reverse the direction of air flow at night.

Desired CO₂ gradients are maintained in each chamber by adjusting blower speed in response to changes in photosynthetically active photon flux density (PPFD; 400–700 nm) and net CO₂ uptake or release by the enclosed ecosystem. Algorithms that incorporate the difference between the measured and desired CO₂ concentrations of air exiting each chamber and, during daylight, the direction and magnitude of change in PPFD are used to vary blower speed independently in each chamber. Blower speed is regulated by varying the DC voltage supplied to each blower motor by a motor controller operating on 115 V AC. Incident PPFD is measured with silicon photodiodes mounted atop blower housings.

During daylight hours, pure CO₂ is injected into air introduced into the south end of one chamber (superambient chamber) to increase the initial CO₂ concentration to 550 μmol mol⁻¹. A CO₂ gradient from 550 to 350 μmol mol⁻¹ is maintained. Ambient air (about 350 μmol mol⁻¹ CO₂) is introduced from the south of the second chamber (subambient chamber) to initiate a daytime CO₂ gradient from 350 to 200 μmol mol⁻¹. It was not feasible to chemically scrub CO₂ from the large volume of air required to maintain this subambient CO₂ concentration at night. Instead, night-time CO₂ concentrations are regulated at about 150 μmol mol⁻¹ above daytime values along each chamber. Ambient air is introduced into the north end of the subambient chamber at night. Pure CO₂ is injected into air blown from the north of the superambient chamber at night to increase

the initial CO₂ concentration to 500 µmol mol⁻¹. Algorithms in a micrologger are used to vary the rate of CO₂ injection in this chamber as a function of blower speed.

Two infrared gas analysers (IRGAs; Table 1) are used to monitor the CO₂ concentrations and dew-point temperatures of the air in each chamber. One analyser per chamber measures CO₂ and water vapour in entering and exiting air. Measurements alternate between the chamber entrance and exit every 1 min. A second analyser per chamber is used to measure CO₂ concentration and water vapour in air along the 50-m vegetated length. Measurements begin in the 5-m compartment at the south of each chamber and proceed toward the northernmost compartment. Air is sampled first from the southern extreme and then from the northern extreme of each compartment. Each measurement requires 1 min. IRGAs are housed in an air-conditioned trailer located 30 m east of the southern extreme of the chambers. Air samples are drawn to the trailer through Teflon tubing (3 mm I.D.) with vacuum pumps. IRGAs are calibrated daily against three CO₂ gas standards and monthly against a dew-point generator. The CO₂ readings are corrected for atmospheric pressure measured with a pressure indicator. Air temperatures at the southern and northern extremes of each 5-m compartment are measured every 15 s with fine-wire (0.5 mm) thermocouples.

Wind speed and direction, global radiation, dry bulb temperature and relative humidity are measured 20 m east of chambers by a weather station. Precipitation is measured using a tipping bucket gauge.

CONTROL OF AIR TEMPERATURE AND HUMIDITY

A major objective of environmental control in this system is to suppress increases in air temperature and water vapour that occur along chambers during daylight. This is accomplished by cooling and dehumidifying air at 5-m intervals along each chamber. Gradients in air temperature and water vapour that normally develop in semi-closed chambers like these are reduced to smaller gradients that develop along each 5-m compartment.

A mixture of water and ethylene glycol is pumped continuously through coils by a recirculating heat exchanger. Each chamber is serviced by a different heat exchanger. These units are capable of regulating coolant at temperatures of 2–25 °C, and have a cooling capacity of 75 kW at a coolant temperature of 25 °C.

Our goal is to approximate the ambient temperature in each compartment, so incoming air is cooled below the ambient temperature and exiting air is slightly warmer than ambient. The cooling capacity required to approach ambient temperature varies diurnally and seasonally. During 1998, changes in required cooling were accommodated by manually adjusting controls

on heat exchangers to vary the temperature of coolant supplied. Temperature control was subsequently improved by using the difference between measured (chamber) and desired (ambient) temperatures to adjust the temperature controller of the heat exchanger automatically. Cooling requirements vary among compartments because of differences in transpiration and air flow rates. These differences are accommodated by manually adjusting gate valves that control the flow of coolant to individual coils.

Small rotary fans directed to blow air upwards are positioned 0.5 m above the soil surface near the air entrance and exit and in the centre of each 5-m compartment. Fans reduce stratification of air and ensure that air is mixed before measurements of temperature and gas concentrations.

DATA ACQUISITION AND STORAGE

Microloggers function as interactive controllers and as the initial point of data storage in this system. Every 2 h, accumulated data are transferred from microloggers to personal computers (PC) for permanent storage. Software from Campbell Scientific (Logan, UT) is used to interface microloggers with PCs, and to update screen displays on PCs with 'last-reading' measurements of CO₂ concentration and air and dew-point temperatures from sampling locations.

The atmospheric vapour pressure deficit (vpd) at the air entrance and exit of each 5-m compartment is calculated from 20-min averages of dew-point and dry bulb temperatures. Mean air temperature and vpd per compartment are calculated each 20 min by averaging measurements at the air entrance and exit.

Results

CO₂ GRADIENT

Control of a daytime CO₂ gradient with this system depends on photosynthesis. The rate of air flow through each chamber is independently and automatically adjusted so that net uptake of CO₂ by the 50 m² of enclosed grassland depletes the CO₂ concentration to the desired minimum at the air exit of chambers. One concern with this approach was whether desired CO₂ gradients could be maintained during periods of little rainfall, when photosynthetic rates typically decline, and during the early growing season, when leaf area and PPFD are small. For the ecosystem studied, the enclosed surface area of 50 m² proved more than adequate for regulating CO₂ during the 1998 growing season. Desired CO₂ gradients were maintained for virtually the entire 9-month growing season (March–November), including a 6-month period from March to August when precipitation was 46% of the 85-year mean (452 mm) at this site. Regulation of CO₂ gradients was achieved in early March on days

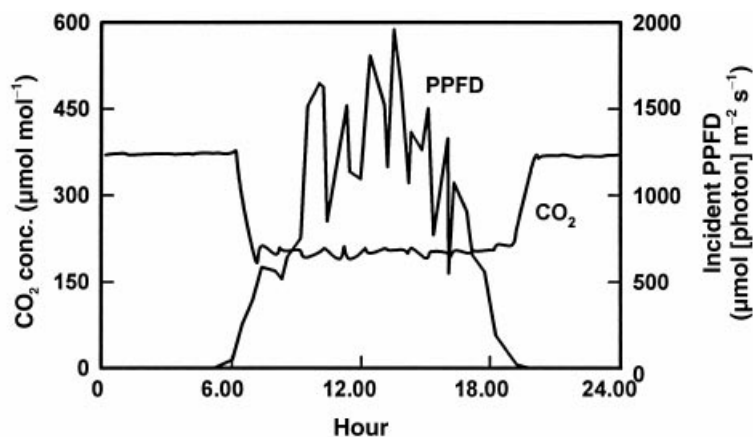


Fig. 3. Diurnal course of CO_2 concentration at the northern extreme (low CO_2 extreme) of the subambient chamber and PPFD measured outside the chamber.

when midday PPFD averaged 25% of that on clear days later in the season. Air flow rates in early March were about 20% of those required during mid-season.

Clouds can cause rapid fluctuations in light and photosynthesis, and so pose one of the greatest challenges to CO_2 control with this system. Algorithms that use only the difference between measured and desired CO_2 concentration to regulate air flow rates provide poor control of CO_2 on days with intermittent clouds. Control is greatly improved by incorporating a 'feedforward' adjustment that is calculated from the direction and magnitude of change in PPFD. With this addition, micrologger programs anticipate changes in photosynthesis and make necessary adjustments in blower speed. The effectiveness of this approach is demonstrated by the CO_2 control that was achieved at the northern extreme of the subambient chamber on a day when PPFD fluctuated widely (Fig. 3). The desired CO_2 concentration during daylight was $200 \mu\text{mol mol}^{-1}$. The measured CO_2 concentration on this day in June 1998 averaged $202 \mu\text{mol mol}^{-1}$ ($\text{SD} = 6 \mu\text{mol mol}^{-1}$) during the 11.5 h daylight period. The CO_2 began to decline towards the desired daytime concentration when PPFD reached $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the morning, and was maintained until mean PPFD declined below $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the evening. The direction of air flow was reversed in the evening, and the CO_2 concentration rose to that of outside air ($370 \mu\text{mol mol}^{-1}$). Transitions between daytime and night-time regulation were completed within 1 h.

Gradients in CO_2 concentration during daylight were slightly curvilinear in both subambient and superambient chambers during 1998 (Fig. 4). This trend of greater CO_2 depletion per unit distance over lower concentrations of each gradient is opposite to that expected if net photosynthesis declines at lower CO_2 concentrations. Gradients in CO_2 depletion are also sensitive to changes in air flow rates. Because of air leakage from chambers, air flow rates decline with dis-

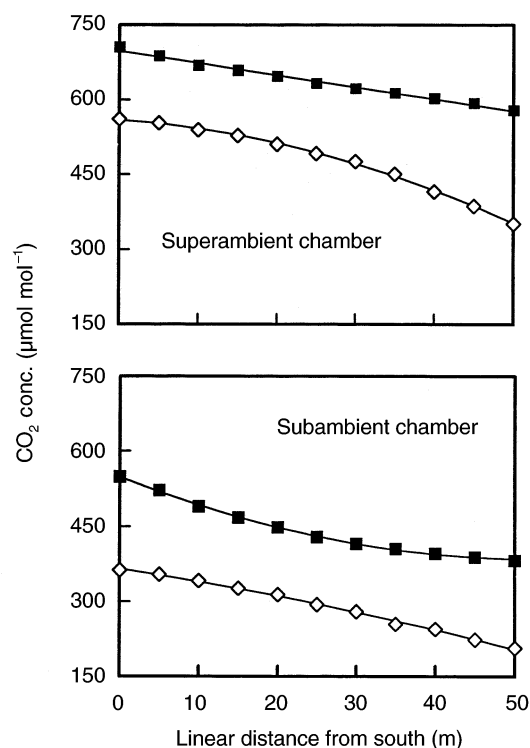


Fig. 4. Mean CO_2 concentration of air along 50-m vegetated lengths of two elongated chambers (superambient and subambient chambers) during the 9-month growing season in 1998 (March–November). Solid lines are regression fits to data for night-time (■) and daylight (◇) periods.

tance from the air entrance of chambers. On 6 July 1998, for example, average rates of air flow, as measured by a thermal anemometer (Model 8455, TSI Inc., St Paul, MN), declined linearly with distance along the subambient chamber. Air flow rates during the daylight period declined from 260 l s^{-1} at the air entrance of the chamber to 75 l s^{-1} at the air exit. A similar decline in air flow rate occurred along the superambient chamber. Curvilinear CO_2 gradients are better explained by the decrease in air flow rates with distance than by changes in photosynthetic rates of enclosed grassland. The direction of air flow is automatically reversed at night. Air is blown from the north end of each chamber, the end with the lowest CO_2 concentration. Night-time gradients were linear or curvilinear, the latter reflecting an increase in ecosystem respiration per unit area with distance along chambers, a decrease in air flow rates with distance, or a combination of the two.

Consistent CO_2 concentrations were maintained along gradients during the 9-month growing season in 1998 despite seasonal variation in species composition, leaf area, precipitation and temperature. Variation in CO_2 concentration was slightly greater at superambient than at subambient concentrations, probably because of the variation introduced by adjusting CO_2 injection rates to blower speed. Between 75 and 86% of CO_2 readings at sampling locations along the

superambient chamber, and between 91 and 97% of CO₂ readings along the subambient chamber, fell within 25 $\mu\text{mol mol}^{-1}$ of the annual mean for the location. Sampling locations near the air exit of the superambient chamber exhibited the greatest variation in CO₂ concentration, but variability in CO₂ did not differ consistently with distance along the subambient chamber. Variation was greater at night when air flow was slower.

The objective of CO₂ control at night was to regulate concentrations at 150 $\mu\text{mol mol}^{-1}$ above daytime values along each gradient. This objective was better achieved in the subambient than the superambient chamber (Fig. 4). CO₂ concentrations in the subambient chamber were 135–185 $\mu\text{mol mol}^{-1}$ greater during the night than during daylight hours. The day/night difference in CO₂ was greatest at the north end of the subambient chamber where ambient air is introduced at night and CO₂ concentration is not controlled. The greatest day/night difference in CO₂ concentration in the superambient chamber occurred at the north end, where air is enriched with CO₂ at night. The reduced control of night-time CO₂ concentration at this location reflects the difficulty encountered during early to mid-season in adjusting CO₂ injection rates for natural variation in the CO₂ concentration of introduced air.

TEMPERATURE AND HUMIDITY CONTROLS

The goal of environmental control was to regulate temperature and water vapour within ranges that are realistic, and to minimize environmental differences among CO₂ treatments. This was accomplished by dividing gradients in air temperature and water vapour that develop during daylight into a series of smaller, repeated gradients. Effectively, this results in division of each 60-m long chamber into an interconnected series of smaller (5-m long) compartments in which CO₂ concentrations differ, but mean air temperature and vpd are similar.

Daytime temperatures in chambers tracked the seasonal pattern in 1998, but were slightly (2–4 °C) cooler than ambient during the warmest part of the year (Fig. 5). Air temperatures were similar in superambient and subambient chambers. A recent programming addition to vary the temperature of coolant when chamber and ambient temperatures deviate should improve the match between these temperatures and reduce temperature differences between chambers. Compartment-to-compartment variation in temperature, assessed as the standard deviation of daytime means among compartments, increased as ambient temperature rose (Fig. 6).

Gradients in dry bulb temperature between points of air entrance and exit in individual compartments vary with changes in air flow rates, transpiration rates and net radiation. Temperature gradients tend to increase as ambient or outdoor temperature rises (Fig. 6),

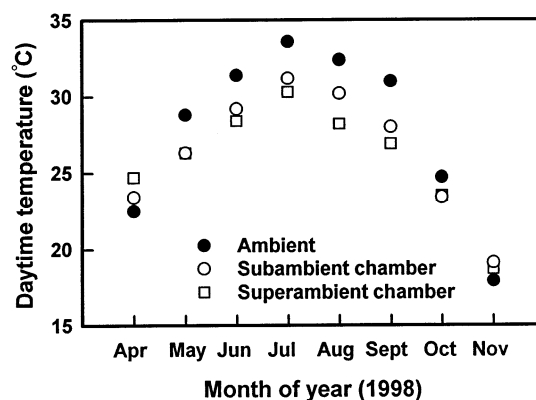


Fig. 5. Daytime air temperature averaged by month and over the 10 5-m long compartments in subambient (○) and superambient (□) chambers and temperature measured outside chambers (●, ambient). Temperatures from March were not stored.

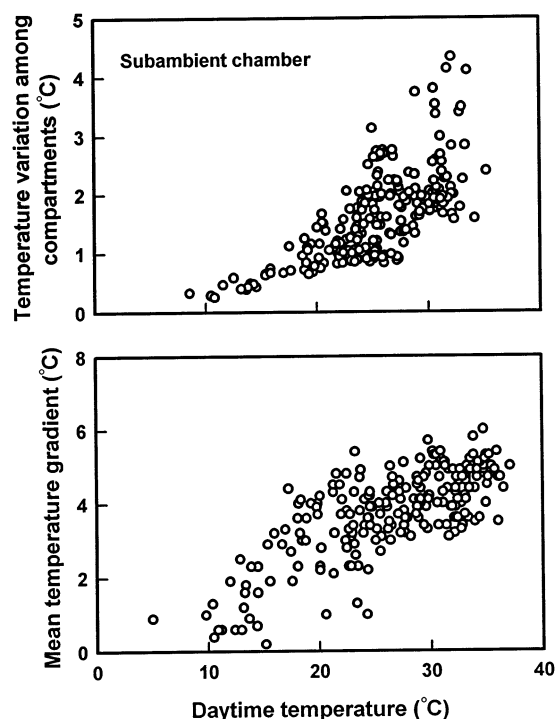


Fig. 6. (a) Standard deviation in mean (entrance/exit) daytime temperature among the 10 5-m long compartments in the subambient chamber as a function of average daytime temperature across all compartments (upper panel). (b) The relationship between the mean gradient in daytime air temperature along the 5-m long compartments in the subambient chamber and daytime temperature measured outside the chamber. Each point represents data for a single day during the 1998 growing season. Relationships of temperature gradients and variation in mean temperature were similar in the superambient chamber.

apparently because the increase in net radiation during the warmest part of the year is not completely dissipated by accompanying increases in transpiration rates and faster air flow.

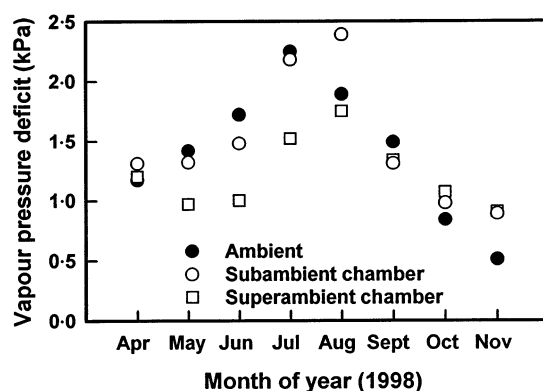


Fig. 7. Daytime vapour pressure deficit of air (vpd) averaged by month and over the 10 5-m long compartments in superambient (\square) and subambient (\circ) chambers and vpd measured outside chambers (\bullet , ambient).

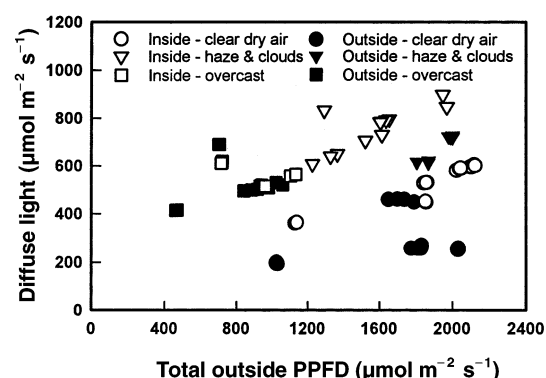


Fig. 9. Relationship of diffuse light measured inside and outside chambers under different sky conditions to total PPFD.

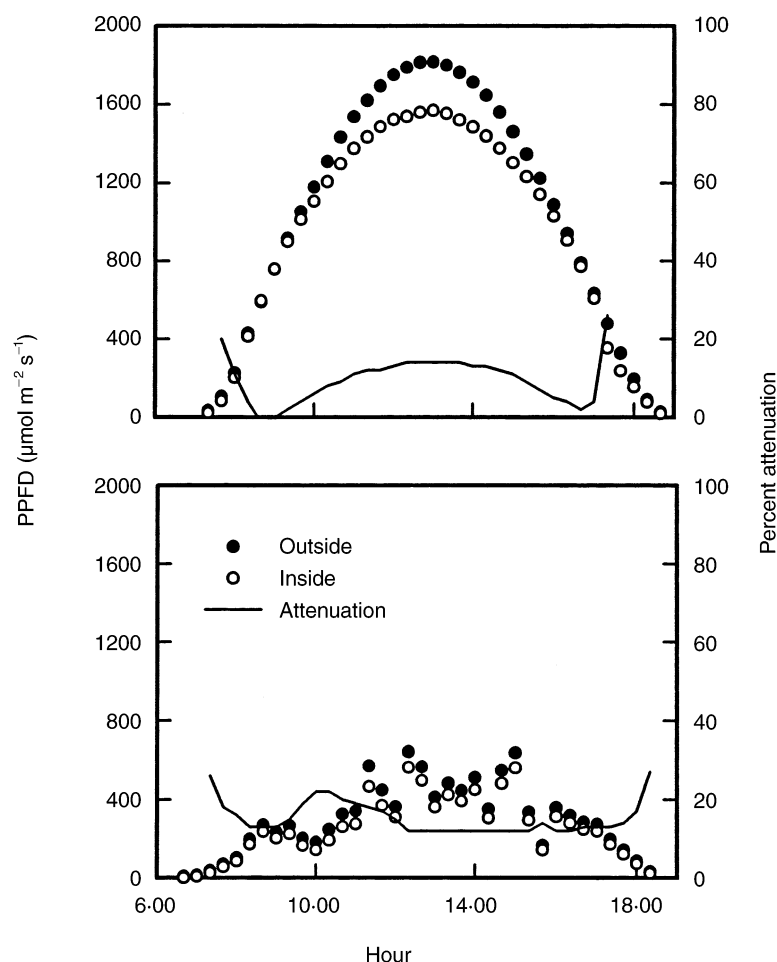


Fig. 8. Intensity of PPFD inside and outside CO_2 chambers and percentage attenuation of PPFD by the polyethylene covering of the chamber on representative (a) clear and (b) cloudy days.

deviation occurred during the mid-summer months (June–August) when temperatures were warmest. Between-chamber differences in vpd were also greatest during summer. Mean vpd was nearly identical in subambient and superambient chambers during the cooler spring and autumn months.

LIGHT REGIME

Chambers were oriented along a north–south gradient and structural supports were minimized to provide uniform light conditions. Attenuation of PPFD by the polyethylene film was measured with 1-m long-line quantum sensors (LI-191SA, Li-Cor Inc., Lincoln, NB, USA). Sensors were placed above plants and across the 1-m width of chambered plots along an east–west axis. The polyethylene covering transmits 85–95% of incident PPFD under most conditions (Fig. 8), but usually increases both the absolute and relative amounts of diffuse light (Fig. 9). Diffuse light, as measured in the centre of chambers with the SunScan canopy analysis system (Delta-T Devices, Cambridge, UK), varies with sky conditions and sun angle. The diffuse component of PPFD in chambers ranges from 30% on clear, dry days to up to 70% on humid days. Diffuse light usually ranges from 15 to 50% of total PPFD outside chambers. Only on heavily overcast days, when the diffuse component of light exceeds 60%, does the chamber effect disappear.

Discussion

The unique chambers described here provide reproducible control of CO_2 along a continuous gradient from superambient to subambient concentrations. A particular advantage of this approach is that it provides information on recent and near-term responses of ecosystems to CO_2 that are not available from other field studies. To our knowledge, this also is the only field facility available for controlling CO_2 at subambient concentrations on large field plots for extended periods (years). Chemicals used in laboratories

In this, as in most field chambers used for CO_2 research, water vapour is not directly regulated. Consequently, vpd sometimes deviates from ambient and can differ between chambers (Fig. 7). The greatest

and glasshouses to deplete CO₂ are not a viable option for extended field experiments in which massive quantities of air are processed. Smaller field plots (about 2 m²), however, can be exposed to subambient CO₂ with chambers that employ 'closed-loop' air circulation systems (Allen *et al.* 1992).

Although originally designed to maintain subambient CO₂ concentrations (Mayeux *et al.* 1993), this system was rather easily adapted for CO₂ enrichment studies. Its notable advantage for this purpose is the minimal cost of injection gas required. During 1998, we used almost 1900 kg of pure CO₂ to enrich 50 m² of grassland by an average of 100 µmol mol⁻¹ for 24 h day⁻¹ over 9 months (superambient chamber). Expressed per m² of grassland enriched, the annual CO₂ requirement was 38 kg. The total annual expense for CO₂ injected was \$785. The amount of CO₂ required to enrich the same area of vegetation using open-top chambers (OTC) or free-air CO₂ enrichment (FACE) systems would be at least an order of magnitude greater. Kimball (1992) calculated annual CO₂ requirements for operating OTC and FACE systems of 1.86 and 4.12 t m⁻² of enriched surface area, respectively, assuming CO₂ enrichment of 300 µmol mol⁻¹ for 24 h day⁻¹ over 6 months. Scaled proportionally for the conditions of our experiment (100 µmol mol⁻¹ rather than 300 µmol mol⁻¹ enrichment and 9 months instead of 6 months), annual CO₂ requirements of OTC and FACE systems would be 0.93 and 2.1 t m⁻². A trade-off for the economical use of CO₂ is the greater cost of electrical power required to cool chambers. For the 12-month period that included the 1998 growing season, 288 000 kW-h of electrical power was used to operate elongated chambers and associated equipment and to air-condition the trailer that houses computers and IRGAs. This computes to an annual power requirement of 2880 kW-h m⁻² (100 m² total) of grassland studied. The power requirements of OTC and FACE systems are largely those associated with operating blowers. Kimball (1992) estimated annual power requirements of 360 and 30 kW-h m⁻² included in OTC and FACE studies, respectively (including areas exposed to ambient CO₂). Scaling to 9 months instead of the 6 months used by Kimball (1992) yields annual electrical requirements of about 540 and 45 kW-h m⁻² of study area for OTC and FACE systems, respectively.

Imposed on the CO₂ gradient maintained in chambers is a series of sequential temperature and water vapour gradients. While not ideal, increases in temperature that occur within 5-m lengths approximate changes encountered in open-top chambers (Leadley & Drake 1993; Ham *et al.* 1995), and can be maintained without the fast turnover rates of air that are required in open-top chambers. In this application, average temperatures in 5-m compartments are controlled to approximate those outdoors. Control has been improved by incorporating an active feedback between the temperature measured inside chambers and the temperature of

the coolant. With this improvement, chambers should also be capable of regulating air temperatures that are below or above ambient values, control that is lacking in most open-top chambers (but see Norby *et al.* 1997; Van Oijen *et al.* 1998).

Whether gradients in temperature and water vapour significantly affect biomass production or other characteristics of plants must be examined. If plant properties vary consistently with position along 5-m compartments, it may be necessary to consider compartments as experimental units and the mean CO₂ concentrations of compartments as the independent variable in regression analysis of CO₂ effects.

Physiological studies are rather easily accommodated in elongated chambers. Zippered openings (each 0.5 m long) were added to the polyethylene covering of each 5-m compartment (at about 0.4 m height) to provide access for measurements of leaf water potential and gas exchange and soil respiration. Canopy fluxes of CO₂ and water vapour can also be calculated from measurements of CO₂ concentration and air dew-point and dry-bulb temperatures that are taken at the beginning and end of each 5-m compartment when information on air flow rates is available (e.g. Polley *et al.* 1993). Preliminary calculations indicate that enrichment of CO₂ by 150–200 µmol mol⁻¹ increased net photosynthesis of grassland by about 30%. Net uptake of CO₂ during daylight was estimated separately for the subambient and superambient chambers as the product of average fan speed (a surrogate for air flow rate) and CO₂ depletion over the 50-m vegetated length of each chamber. The ratio of these values (superambient/subambient) was calculated daily, and averaged 1.33 over 27 days (September–November 1997) shortly after CO₂ control was initiated. Chambers thus can be used to address the important issue of how leaf gas exchange scales to the canopy level.

Although CO₂ gradients were not replicated here, the approach described has the advantage of providing information on the shape of plant and ecosystem responses to a large gradient in CO₂ concentration. The paucity of experimental information on response curves is a major hindrance to projecting the timing and nature of CO₂ effects (Körner 1995). Elongated chambers thus fill a void in CO₂ research facilities by enabling the study of trends in plant and ecosystem responses to CO₂ over both subambient and superambient concentrations.

Acknowledgements

Tommy Greeson helped construct and maintain chambers. Data were collected and graphed by Anne Gibson and Katherine Jones. Comments from Hartwell Allen, Laural Anderson, Justin Derner, Bert Drake and Robert Jackson improved the manuscript.

References

- Ackerly, D.D. & Bazzaz, F.A. (1995) Plant growth and reproduction along CO₂ gradients: non-linear responses

- and implications for community change. *Global Change Biology* **1**, 199–207.
- Alcamo, J., Kreileman, G.J.J., Bollen, J.C., van den Born, G.J., Gerlagh, R., Krol, M.S., Toet, A.M.C. & de Vries, H.J.M. (1996) Baseline scenarios of global environmental change. *Global Environmental Change* **6**, 261–303.
- Allen, L.H. Jr, Bisbal, E.C., Boote, K.J. & Jones, P.H. (1991) Soybean dry matter allocation under subambient and superambient levels of carbon dioxide. *Agronomy Journal* **83**, 875–883.
- Allen, L.H. Jr, Drake, B.G., Rogers, H.H. & Shinn, J.H. (1992) Field techniques for exposure of plants and ecosystems to elevated CO₂ and other trace gases. *Critical Reviews in Plant Sciences* **11**, 85–119.
- Baker, J.T., Allen, L.H. Jr & Boote, K.J. (1990) Growth and yield responses of rice to carbon dioxide concentration. *Journal of Agricultural Science, Cambridge* **115**, 313–320.
- Dippery, J.K., Tissue, D.T., Thomas, R.B. & Strain, B.R. (1995) Effects of low and elevated CO₂ on C₃ and C₄ annuals. I. Growth and biomass allocation. *Oecologia* **101**, 13–20.
- Ehleringer, J.R., Cerling, T.E. & Helliker, B.R. (1997) C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* **112**, 285–299.
- Ham, J.M., Owensby, C.E., Coyne, P.I. & Bremer, D.J. (1995) Fluxes of CO₂ and water vapour from a prairie ecosystem exposed to ambient and elevated atmospheric CO₂. *Agricultural and Forest Meteorology* **77**, 73–93.
- Hendrey, G.R., Ellsworth, D.S., Lewin, K.F. & Nagy, J. (1999) A free-air enrichment system for exposing tall forest vegetation to elevated atmospheric CO₂. *Global Change Biology* **5**, 293–309.
- Johnson, H.B., Polley, H.W. & Mayeux, H.S. (1993) Increasing CO₂ and plant–plant interactions: effects on natural vegetation. *Vegetatio* **104/105**, 157–170.
- Kimball, B.A. (1992) Cost comparisons among free-air CO₂ enrichment, open-top chamber, and sunlit controlled-environment chamber methods of CO₂ exposure. *Critical Reviews in Plant Sciences* **11**, 265–270.
- Körner, Ch. (1995) Towards a better experimental basis for upscaling plant responses to elevated CO₂ and climate warming. *Plant, Cell and Environment* **18**, 1101–1110.
- Leadley, P.W. & Drake, B.G. (1993) Open top chambers for exposing plant canopies to elevated CO₂ concentration and for measuring net gas exchange. *Vegetatio* **104/105**, 3–15.
- Leadley, P.W., Niklaus, P.A., Stocker, R. & Körner, Ch. (1997) Screen-aided CO₂ control (SACC): a middle ground between FACE and open-top chambers. *Acta Oecologia* **18**, 207–219.
- Mayeux, H.S., Johnson, H.B. & Polley, H.W. (1991) Global change and vegetation dynamics. *Noxious Range Weeds* (eds L. F. James, J. O. Evans, M. H. Ralphs & R. D. Child), pp. 62–74. Westview Press, Boulder, CO.
- Mayeux, H.S., Johnson, H.B., Polley, H.W., Dumesnil, M.J. & Spanel, G.A. (1993) A controlled environment chamber for growing plants across a subambient CO₂ gradient. *Functional Ecology* **7**, 125–133.
- Mayeux, H.S., Johnson, H.B., Polley, H.W. & Malone, S.R. (1997) Yield of wheat across a subambient carbon dioxide gradient. *Global Change Biology* **3**, 269–278.
- Norby, R.J., Edwards, N.T., Riggs, J.S., Abner, C.H., Wullschlegel, S.D. & Gunderson, C.A. (1997) Temperature-controlled open-top chambers for global change research. *Global Change Biology* **3**, 259–267.
- Phillips, O.L. & Gentry, A.H. (1994) Increasing turnover through time in tropical forests. *Science* **263**, 954–958.
- Polley, H.W., Johnson, H.B. & Mayeux, H.S. (1992) Growth and gas exchange of oats (*Avena sativa*) and wild mustard (*Brassica kaber*) at subambient CO₂ concentrations. *International Journal of Plant Sciences* **153**, 453–461.
- Polley, H.W., Johnson, H.B., Mayeux, H.S. & Malone, S.R. (1993) Physiology and growth of wheat across a subambient carbon dioxide gradient. *Annals of Botany* **71**, 347–356.
- Polley, H.W., Johnson, H.B., Mayeux, H.S., Brown, D.A. & White, J.W.C. (1996) Leaf and plant water use efficiency of C₄ species grown at glacial to elevated CO₂ concentrations. *International Journal of Plant Sciences* **157**, 164–170.
- Street-Perrott, F.A., Huang, Y., Perrott, R.A., Eglinton, G., Barker, P., Khelifa, L.B., Harkness, D.D. & Olago, D.O. (1997) Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science* **278**, 1422–1426.
- Van Oijen, M., Schapendonk, A.H.C.M., Jansen, M.J.H., Pot, C.S., Van Kleef, J. & Goudriaan, J. (1998) Effects of elevated CO₂ on development and morphology of spring wheat grown in cooled and non-cooled open-top chambers. *Australian Journal of Plant Physiology* **25**, 617–626.

Received 14 June 1999; revised 31 August 1999; accepted 13 September 1999